THE SPARGANIACEAE IN THE SOUTHEASTERN UNITED STATES[1]

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SPARGANIACEAE Rudolphi, Syst. Orb. Veg. 27. 1830, nom. cons.

(BUR-REED FAMILY)

A monogeneric family of perennial, rhizomatous, monoecious, marsh or aquatic, herbaceous monocotyledons distinguished by distichous, linear, sheathing leaves; simple or branched stems; flowers in dense, globose heads on the upper part of the stem or on the branches, the staminate heads distal to the carpellate; perianth of 1–6 tepals; carpellate flowers with 1 ovary; and fruit drupelike. TYPE GENUS: *Sparganium*.

Engler grouped Sparganiaceae with Typhaceae and Pandanaceae in the Pandanales, placing the order at the beginning of the monocotyledons. That these families are primitive is an idea that is no longer tenable (indeed, in Wettstein's system they *close* the monocotyledons). Their affinities, however, remain partly unsettled. Sparganiaceae and Typhaceae, now generally considered to be the sole families of Typhales, are so closely related that they may even be confamilial (see below), but their relationship to Pandanaceae is equivocal. One suggestion is that they are "very closely related to Pandanales" and have "a common origin" (Takhtajan); another, that "whatever similarity there is between . . . Pandanaceae and . . . Typhales reflects parallelism or convergence, rather than inheritance from a common ancestry" (Cronquist, 1981; see also Hutchinson, and Thorne). (For further discussion, see Briggs & Johnson; Cronquist; Harada; Mallick & Sharma; Sharma; and Takhtajan.)

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Hutchinson regarded the Typhales as "a reduced and very advanced group derived from the Liliaceous stock, not through the Araceae, but perhaps from the same stock that has also given rise to the Xanthorrhoeaceae. . . . "

Rejecting liliaceous ancestry for the order, Cronquist considered it to be "a separate line from a generalized commelinalean ancestry, parallel in some respects to the other groups with reduced flowers." His assignment of Typhales to the Commelinidae followed the "arguments of stomatal organization [stomata with two subsidiary cells (Stebbins & Khush), thus differing from Liliaceae, which have no subsidiary cells] and vessel distribution [vessels in all vegetative organs; vessels of Liliaceae are confined chiefly to the roots]. . . . " Further, Typhales have starchy endosperm, which is "standard in the Commelinidae but rare in the Liliales."

Thorne characterized the Typhales as "little more than anemophilous, palustrine aroids." He placed them in his Arales, consisting of Araceae, Lemnaceae, and Typhaceae (including *Sparganium*). In this connection, it is of interest to note that the rust *Uromyces Sparganii* C. & P. has both *Sparganium eurycarpum* and an aroid, *Acorus Calamus* (see Savile), as the hosts of its perfect stage; some think that this indicates relationship between these two angiosperms.

Pre-Englerian authors placed *Sparganium* and *Typha* together in the Typhaceae. The tradition of separating these genera as different families was started by Engler and followed by almost all subsequent workers until recently, when D. Müller-Doblies reexamined the relationship between the genera. He concluded that "the five different characters by which Engler justified the family Sparganiaceae are wrong or, in two cases, without any significance. . . . The few remaining but very obvious differences may be explained to a large extend [*sic*] as an adaptation of *Typha* to anemochory. They are far beyond [i.e., below] the minimum of differences required for separated families. The family Sparganiaceae is dropped and the Typhaceae s.l. have been described." The two taxa *are* similar in many ways: ecologically, cytologically, chemically, embryologically, and morphologically; their union in one family (by post-1970 authors, for example, Casper & Krausch; D. Müller-Doblies; U. Müller-Doblies; Takhtajan; and Thorne) may now — but for tradition — be difficult to gainsay.

1. **Sparganium** Linnaeus, Sp. Pl. **2:** 971. 1753; Gen. Pl. ed. 5. 418. 1754.

Perennial, rhizomatous, monoecious, marsh or aquatic, herbaceous plants with fibrous roots. Stems emersed [or floating], simple or branched. Leaves basal and cauline, submersed, floating, or emersed, sessile, distichous, linear, sheathing, more or less flattened to V-shaped or triangular in cross section, with many longitudinal veins, these connected ladder-runglike by cross diaphragms; stomata paracytic. Inflorescences of globose, many-flowered heads on the upper part of the stem and on the branches, inflorescence axis more or less zigzag; staminate and carpellate heads separate, the branches sometimes bearing only staminate heads; staminate heads distal, soon falling, the naked axis usually persisting; carpellate heads proximal, those of the

main stem axillary or supra-axillary to leafy bracts. Each flower subtended by a bract that is sometimes difficult to distinguish from the tepals. Staminate flowers with 1–6 tepals; androecium of 1–8 stamens, sometimes with partly united filaments; anthers 4-sporangiate, introrse to extrorse, the tapetum amoeboid at first, later periplasmodial, the pollen monoporate, more or less spheroidal or ellipsoid, binucleate when shed. Carpellate flowers with (2 or) 3 or 4 (or 5) persistent tepals; gynoecium of 1 (or 2) [3] carpels, usually pseudomonomerous; stigma 1 (or 2) [3]; style 1, usually persisting as a beak on the fruit; ovary 1- (or 2-) [3-]locular, the locule with a single bitegmic, crassinucellar, anatropous, pendulous ovule, the outer integument longer than the inner; megagametophyte development of the Polygonum type; endosperm Helobial in development. Fruits drupelike, crowded in a burlike head, the exocarp spongy, the endocarp hard and with a "germination pore" at its distal end, the inner opening of the pore occluded by a "micropylar cap" or "plug" derived through enlargement of the micropylar part of the integuments; seeds with starchy endosperm and large, straight embryo. TYPE SPECIES: *S. erectum* L.; see P. A. Rydberg, N. Am. Fl. **17:** 5. 1909. (Name from Greek, *sparganion,* a swaddling band, in apparent allusion to the long, narrow leaves.)—BUR-REED.

A genus of about 15 species, primarily North Temperate but also in the Arctic, extending in the New World from Alaska, the Mackenzie Delta, Hudson Bay, and Greenland, south to the southern United States and Baja California; and in the Old World from Iceland and northern Eurasia, south to northern Africa, Turkey, Iran, Afghanistan, Assam, China, and Japan; also Indonesia (Sumatra and New Guinea), eastern Australia, and New Zealand.

About nine species of *Sparganium* are known in North America. The three in the southeastern United States belong to subgenus XANTHOSPARGANIUM Holmb. (perianth segments thin, uniformly light brown; seeds without longitudinal ridges). *Sparganium americanum* Nutt. occurs throughout our area (see distribution map in Beal, 1960, supplemented by Mississippi records in Jones), growing in shallow water or on wet shores of ponds, streams, and swamps. Beal (1960) described *S. americanum* as "a complex polymorphic species exhibiting extensive variation in height, leaf width, thickness and texture, degree of branching of the inflorescence, position of pistillate heads, size of fruit and length of style and stigma." He distinguished two "well defined" races: (1) the "coastal race," of Coastal Plain distribution, characterized by stigmas 1.5 mm or more long, leaves "wide for the species," and inflorescence branches two to five; and (2) the "Appalachian race," of Appalachian and Ozarkian distribution, characterized by stigmas 0.9 mm or less in length, leaves "narrow for the species," and inflorescence simple to sparingly branched. The races overlap morphologically, with intermediate plants (the "ubiquitous race") scattered throughout the range of the species.

In much the same habitats as *Sparganium americanum* but of limited distribution in the Southeast are *S. androcladum* (Engelm.) Morong, reported in our area only from western North Carolina (Beal, 1960) and northwestern

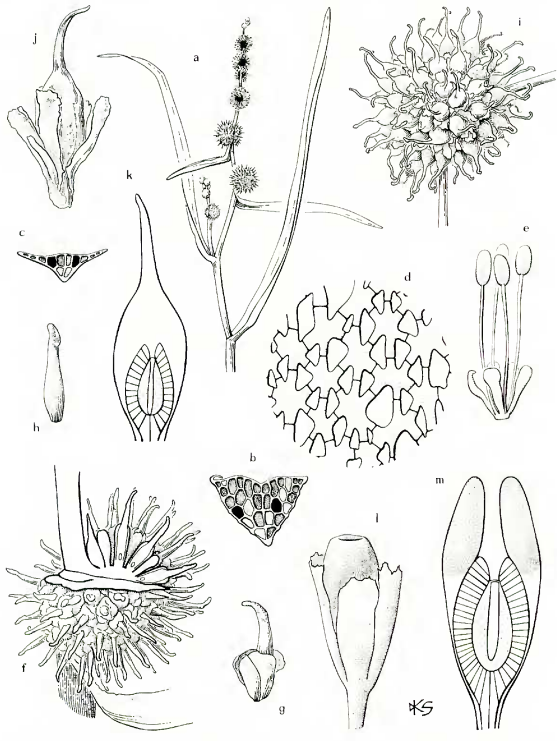

FIGURE 1. **Sparganium.** a–m, *S. americanum:* a, tip of flowering stem with axillary branch, the staminate heads distal to the larger, carpellate ones, × ½; b, diagrammatic cross section of leaf near base showing diaphragms (stippled) surrounded by supporting tissue, × 3; c, same, near tip of leaf, × 3; d, detail of diaphragm to show individual cells (lightly shaded) and air spaces (unshaded), × 150; e, staminate flower with tepals and stamens, × 6; f, carpellate inflorescence (¼ removed) subtended by bract, immediately after anthesis, × 3; g, carpellate flower with gynoecium and tepals, × 6; h, gynoecium, × 6; i, infructescence, × 2; j, fruit with persistent perianth, × 5; k, diagrammatic vertical section of fruit, endocarp hatched, endosperm

Louisiana (MacRoberts), and *S. chlorocarpum* Rydb.,[2] reported by Beal from eastern Tennessee.

According to Beal, reports of *Sparganium eurycarpum* Engelm., $2n = 30$, subgenus SPARGANIUM (subgen. *Melanosparganium* Holmb.) (perianth segments thick, with dark brown to black apex; seeds with 6–10 longitudinal ridges), from the Southeast as far south as Florida, are based on misidentification of robust plants of *S. americanum*.[3]

Some species of *Sparganium* are distinctive; others seem not to be. Many characters used to distinguish taxa in the genus are (as in many other aquatic plants) inconstant or readily altered by environment. According to Mason, characters such as presence or absence of supra-axillary heads, cross-sectional shape of leaves, position of tepals, and shape of fruits appear to be quite meaningless. Nomenclature of the genus is frustrating. *Sparganium* is much in need of study with the use of modern techniques.

Several hybrids involving about 10 taxa in various combinations have been reported, but apparently none has been verified experimentally. The hybrid *Sparganium emersum* × *S. angustifolium* appears to be fully fertile, but *S. emersum* subsp. *erectum* × *S. erectum* subsp. *neglectum* (= *S. erectum* subsp. *oocarpum*; *S.* × *tardivum* Topa) shows "very poor fertility" (Cook, 1961b). Almost nothing is recorded about breeding behavior of other putative hybrids.

Chromosome counts, some undocumented, are available for many of the species, all of which are diploids with $2n = 30$. In only one instance (Harada) has a different number been reported: $2n = 3x = 45$ in some root-tip cells of *Sparganium stenophyllum*. (Other root tips of this species collected from the same place showed $2n = 30$.)

The fossil record of *Sparganium*, based mostly on fruits, but also on pollen (Muller) and leaves, extends back to the Paleocene (Daghlian). The genus provides an impressive example of evolutionary reduction in the number of locules: *S. multiloculare* of the British Bembridge Beds (Oligocene) had five-, four-, three-, and two-locular forms; forms of *S. ramosum* (i.e., *S. erectum*) from interglacial deposits are four-, three-, or two-locular. The

[2]*Sparganium chlorocarpum* Rydb. is included in the synonymy of *S. emersum* Rehman by Cook (1961b).

[3]The Eurasian *Sparganium erectum* subsp. *erectum* was said by Casper and Krausch to range in the eastern United States south to Florida. This report apparently rests on Cook's suggestion (1961b) that *S. eurycarpum* (attributed to Florida by Cook, Muenscher, Rydberg, and Small, *inter alios*) is seemingly the same as *S. erectum* subsp. *polyedrum* (i.e., subsp. *erectum*). Curiously, though, Casper and Krausch did not include *S. eurycarpum* in the synonymy of *S. erectum*.

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stippled, embryo unshaded, × 6; l, remains of floating fruit collected very late in season, style and central part of fruit above endocarp decayed away, × 6; m, same in vertical section, spongy flotation tissue shaded, endocarp hatched, endosperm evenly stippled, embryo unshaded, × 10.

ovary today is usually one-locular, although in a few species (e.g., *S. erectum* and *S. eurycarpum*) there are typically two locules, occasionally or rarely one or three. Apparently three is the maximum in *Sparganium* today.

Comparative studies of extant species reveal examples of further reduction. Ovaries with two or three locules may show abortion of one or two ovules and may have only one normal locule, the other(s) being rudimentary. One-locular gynoecia may bear a well-developed to rudimentary second stigma, indicating that they are dimerous structures. The dimerous nature is also shown by the vascularization and by the excentric position of the locule (Eckardt). Most of the time, however, one-locular gynoecia show no recognizable remains of an additional carpel. Thus, in *Sparganium* the gynoecia are pseudomonomerous—i.e., they appear to be monomerous in most species but actually incorporate more than one carpel in their make-up or are strictly one-carpellate by reduction from coenocarpous ancestry. In *Sparganium*, "pseudomonomery has reached the last stage of reduction" (D. Müller-Doblies).

Flowers of *Sparganium* are proterogynous and anemophilous. Morphology of the densely many-flowered staminate head is difficult to interpret at anthesis, resulting in despairing and inaccurate descriptions such as that of Fernald (1950), who wrote of the staminate flowers as being "3-androus" and "naked" and as having "minute scales irregularly interposed." That these flowers are composed of one to six tepals and one to eight stamens is confirmed in developmental studies, most recently by U. Müller-Doblies.

The ripe fruits drop into the water, where they can float for at least a year, possibly up to 2.5 years (Guppy, 1897). Eventually the spongy exocarp may rot off, leaving only the endocarp. Dispersal is hydrochorous and both epi- and endozoochorous (mostly by water birds).

At the distal end of the endocarp is a pore through which the embryo emerges in germination. The inner opening of the pore is blocked by a "micropylar plug" ("Samendeckel" of Hegelmaier) formed by enlargement of the integuments (and possibly also the apex of the nucellus; Campbell, 1899). Germination can be delayed as long as several years after maturity, apparently by the restraining influence of the micropylar plug. After decay (?) or removal of the plug, and in a fully saturated atmosphere or under water, germination readily occurs.

Some bur-reeds, but not those of the Southeast, are typically "floating-leaved" species, with flaccid, flat or weakly keeled leaves of obvious dorsiventral internal structure. Others, including those in the Southeast, are typically "emergent" species, with robust, relatively stiff, strongly keeled leaves not obviously dorsiventral. The distinction between the types is not absolute. Kaul (1976) suggested that floating-leaved species are neotenous forms derived from emergent species, a hypothesis supported by the observation that floating seedling-leaves of emergent species are anatomically similar to adult leaves of floating-leaved species. He (1973) regarded *Sparganium* as a genus in transition from the emergent to the floating habit.

In rivers and streams (i.e., in flowing water) emergent species of *Sparganium* such as *S. americanum* may produce completely submersed, sterile

plants, often in dense colonies. The leaves of such plants are ribbonlike and flaccid, resembling those of several other genera (*Alisma, Butomus, Sagittaria, Scirpus,* and *Typha*) that can develop similar underwater leaves (Luther, Voss). Emergent bur-reeds may also produce floating leaves, especially in deeper water.

Bur-reeds are among the plants that can choke waterways, a matter of considerable economic significance in some areas (as in England and Wales; Robson). The fruits of *Sparganium* are important food for water birds; the fruits, stems, and leaves are eaten by mammals (e.g., muskrat, moose). The Klamath Indians of Oregon used the starchy rhizomes of bur-reeds for food (Coville). Certain species of black flies — among the insects most notorious as annoyers of animals and people — choose submersed plants in running water as a larval and pupal substratum; *Sparganium* may rank high among the choices (as in central Maine, where the black fly *Simulium penobscotensis* is a serious summertime nuisance). A few species of *Sparganium* are grown as "bog plants." The unripe fruits of *S. erectum* ("*S. ramosum*") "made into an infusion with sourish red wine and cinnamon" are "good against fluxes of the belly and bleedings of all kinds" (Steinmetz). (The fruits of any other species of bur-reed could probably be used with equal efficacy.)

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